

DESCRIPTIONS OF SCHIZAEACEOUS SPORES TAKEN FROM EARLY CRETACEOUS MACROFOSSILS

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ABSTRACT. Full descriptions are given of spores taken from the original macrofossil material of *Ruffordia goepperti* (Dunk.), *Pelletieria valdensis* Seward, and *Schizaeopsis americana* Berry. All three plants are of Early Cretaceous age, the first two from the Lower Wealden of England, and the last from the Patuxent Formation of the Potomac Group of Virginia, U.S.A. The use of measurements in the erection of species in the dispersed spore genus *Cicatricosisporites* is discussed in the light of these observations.

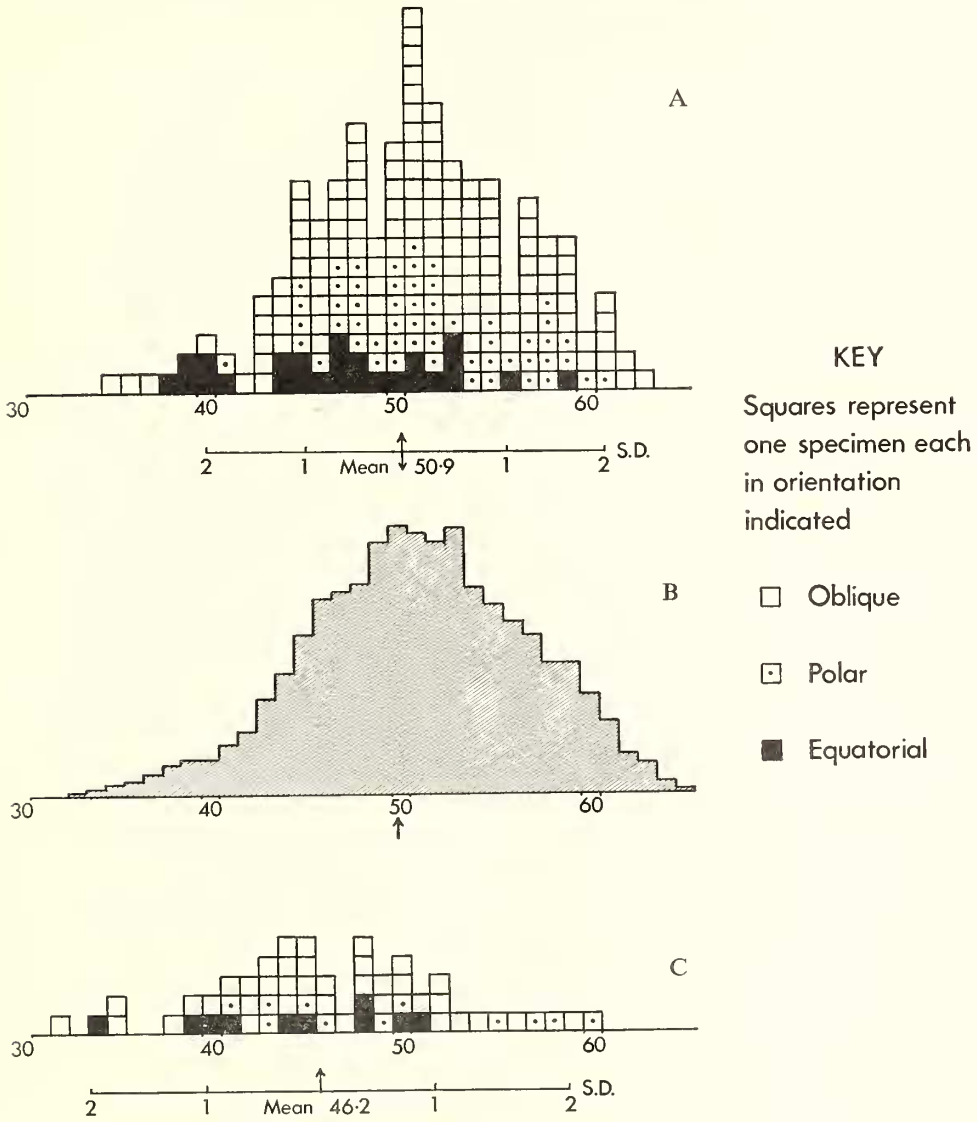
DISPERSED spore palynological studies show that the spore type usually classified as *Cicatricosisporites* Pot. and Gell. first appears in the Early Cretaceous or latest Jurassic, and then diversifies rapidly. Unfortunately these spores have not yet proved to be of great stratigraphical value in the Cretaceous period, and we think this is almost entirely due to the effects of poor typification and description, and of uncoordinated nomenclature. Bolkhovitina (1961) has brought together most of the fossil records of this group in a very useful paper, although her system of nomenclature is unfortunate and many of the figures of other authors which she was obliged to reproduce were inadequate in their original form.

It so happens that three separate fertile plant organ species, believed to belong to the Schizaeaceae, were described with their spores in the period 1911–13. The illustrations of the spores were generalized sketches, with in two cases rather inadequate photographs; and the descriptions do little more than allude to the probable fern family affinity, a treatment which was no doubt considered adequate at the time. Couper (1958) published some photographs of spores of *Ruffordia goepperti* which had been known previously only from Seward's (1913) sketch, but Couper regarded these spores as comparable with his dispersed spore material which he placed in the Eocene species *Cicatricosisporites dorogensis*. As far as we know neither the spores of *Pelletieria valdensis* nor of *Schizaeopsis americana* have been adequately described.

All the material of *Ruffordia* and *Pelletieria* has been kindly loaned for the purpose by the Department of Palaeontology, British Museum (Natural History). The necessary pull from the *Schizaeopsis* specimen was taken during a visit (N.F.H. July 1959) to the United States National Museum, Washington, and permission to figure the material was kindly given later by Dr. F. M. Hueber of that institution. The relevant slide preparations will be sent to the institutions concerned. Potonié (1965, pp. 45–46) refers to this same material which he examined when in Cambridge.

Preparations were made by brief oxidation (approx. two hours) in concentrated nitric acid only, clearance in approx. 5 per cent. ammonia, and mounting unstained in glycerine jelly. In each case all of the material removed from the plant was mounted; it was handled only by pipette and was not centrifuged. Specimens recorded were all

those present on certain selected traverses on the slide preparation. Stage co-ordinates refer to Ortholux microscope no. 491249, Department of Geology, Cambridge.



TEXT-FIG. 1. Frequency distribution histograms of maximum diameter in microns of spores of *Ruffordia goepperti*. A, New preparation (V2192b-f), 200 specimens; standard deviation 5.2μ , coefficient of variation 10 per cent. B, Five point moving average from the data of A. C, Seward's preparation (V2192a), 58 specimens (all available); standard deviation 6.1μ , coefficient of variation 13 per cent.

DESCRIPTIONS

Family SCHIZAEACEAE

Genus RUFFORDIA Seward 1894

Type species. Sphenopteris goepperti Dunker 1846 (Dunker's earlier reference not effective).

Remarks. Although the genus *Ruffordia* was well conceived, Seward should have erected a new species for his relatively good fertile material, instead of relying on the inadequately described holotype (sterile frond) of Dunker. In view of the remarks of Michael (1936, p. 34) a new species may still be necessary, as she could not find in the German specimens the variability which Seward reported. Nomenclatural difficulties would result from any such change now.

Ruffordia goepperti (Dunk.) Seward 1894 (spores)

Plate 43, figs. 1–12

- 1913 Seward, p. 91, text-fig. 2A.
 non 1921 Halle, p. 11, pl. 2, fig. 8.
 1958 Couper, p. 109, pl. 17, figs. 4–6.
 1962 Potonić, p. 104, pl. 10, fig. 268.

Holotype. We have located and figured (Pl. 43, fig. 10) a spore on Seward's slide V2192a which by elimination appears to be the original of his text-fig. 2A (1913); we are considering this spore to be the holotype. Seward's preparation and mounting methods for this material are not known, and the spore is now very pale in colour. The size range and mean of the fifty-eight specimens on his slide differ from those of our preparation (see text-fig. 1c). The spore figured by Couper (1958, pl. 17, figs. 4, 5) is probably another specimen nearby on the slide (OR 48.1 126.1).

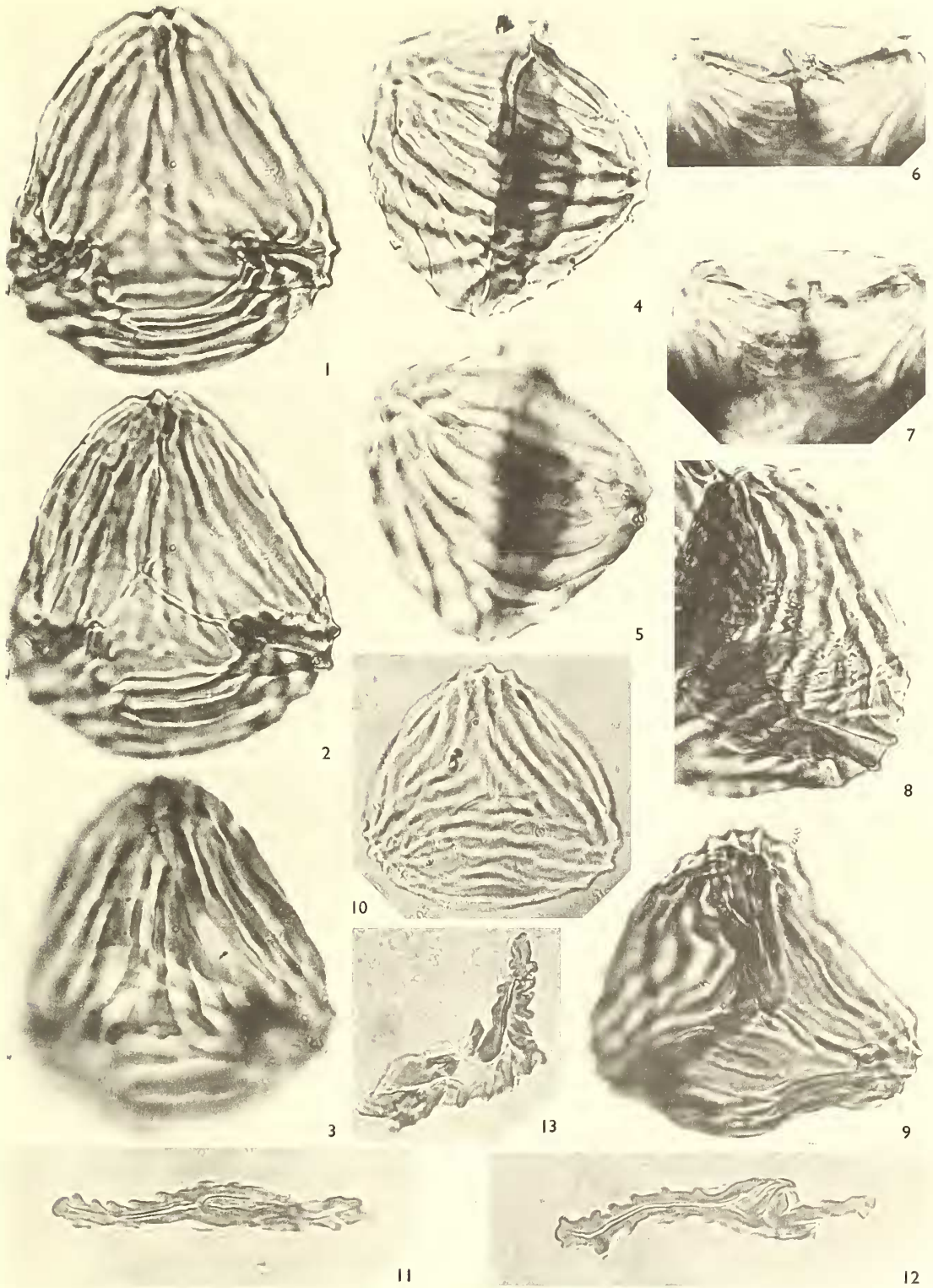
Locality. The specimen V2192A is clearly marked Rufford Collection, Ecclesbourne, nr. Hastings, in spite of Seward's (1913, p. 91) record of Fairlight. The rock is a hard red-brown sideritic siltstone of maximum grain size 50 μ . It is likely to have come from the base of the Ashdown Sands or from the top of Fairlight Clay division *e*.

Material. Spores were taken by needle and by 'pull' from what appeared to be sporangia on the middle section of the frond of specimen V2192A, which according to Museum labels in Seward's handwriting was the specimen he used but did not specifically cite (1913) in making his slide (now V2192a).

Emended spore diagnosis. Spores trilete tetrahedral with strongly convex distal surface, but with rounded triangular amb. Contact faces smooth (Pl. 43, figs. 1–2). The lips are simple membraneous 2–3 μ high extensions of the exine (Pl. 43, fig. 6) which has a constant thickness of 1.5 μ excluding sculpture. The inter-radial equatorial and distal regions bear three sets of sub-parallel muri which occasionally join to form a partial reticulum (Pl. 43, figs. 4, 5, 8). The three sets of muri leave a triangle (Pl. 43, fig. 10) of varying size centred on the distal pole, with variable sub-parallel sculpture within the triangle. Muri, of rounded profile, 1.5–2.0 μ high and wide, spaced on average

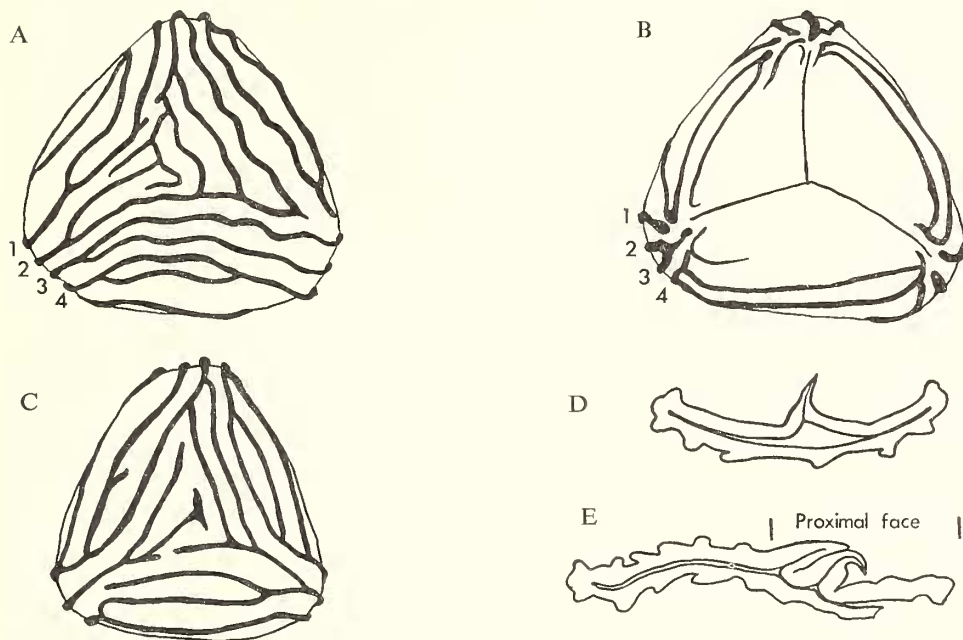
EXPLANATION OF PLATE 43

Figs. 1–12. *Ruffordia goepperti* (Dunk.) Seward; spores taken from specimen V2192A BMNH, $\times 1000$. 1–3, Proximal aspect, high, mid and low focus respectively; prep. V2192c, OR 33.5 108.5. 4–5, Equatorial aspect, mid and low focus; prep. V2192d OR 30.9 120.6. 6–7, Oblique proximal aspect, mid and high focus; Prep. V2192d, OR 32.2 120.3. 8, Oblique aspect pattern of distal muri; prep. V2192c, OR 46.4 117.9. 9, Proximal aspect, showing radial rib profile formerly diagnostic; prep. V2192c, OR 46.4 112.4. 10, Holotype, proximal aspect, low focus (distal); Seward's prep. V2192a, OR 48.2, 127.2. 11, Section perpendicular to polar axis, triplan, distal; prep. V2192g, OR 54 112.4. 12, Adjacent section, showing laesura with compressed lips and proximal face; prep. V2192g, OR 60.1 115.6. 13, Section parallel to polar axis, laesura open; prep. V2192h, OR 40.1 125.1.



2–3 μ apart (Pl. 43, fig. 8). Muri of adjacent sets do not coalesce (see text-fig. 2A–C) in equatorial radial regions which are flexible and not thickened.

Dimensions. Diameter (200 specimens) 35–(51)–63 μ (preparations V2192b–f); 80 per cent. of specimens fall between 44 and 58 μ . Percentage of specimens in polar view 28, equatorial view 13, and oblique 59 as plotted in text-fig. 1A. Similar observations for Seward's slide V2192a are given in text-fig. 1C; the lower values for diameter (58 specimens) 32–(46)–58 μ , 80 per cent. between 39 and 55 μ , may be due to difference in maceration procedure.



TEXT-FIG. 2. *Ruffordia goepperti* (spores), diagrams $\times 1000$; muri shown in black. A–C, from Seward's preparation (V2192a) to illustrate the configuration of the muri. A, Distal; B, Proximal faces of holotype, Plate 43, fig. 10, OR 48.2 127.2. C, Distal face of specimen figured by Couper (1958), OR 48.1 126.1. D, Section normal to laesura, half radial distance from pole, showing concave proximal face and false margo. E, Specimen of Plate 43, fig. 12, showing folded proximal face and false margo.

Description. All spores are strongly compressed and usually folded. Possibly because they were dried out before burial and became concave proximally, there is a tendency for the parts of the exine adjacent to the laesurae to be pressed together; this raises the lips, simulates a margo in some specimens, and causes some proximal rigidity (text-fig. 2A; Pl. 43, figs. 6, 12, 13). The arrangement of muri in the radial region is comparable with that shown by Dettmann (1963, text-fig. 4p); the mode of preservation however, always causes difficulty in observing details of the radial areas.

Comparison. The spores obtained from *R. goepperti* (Halle 1921) from an unspecified horizon in Ussuri appear from poor illustrations to be of a different type.

Remarks. Groot and Penny (1960) combined the spores of Seward and Couper in the dispersed spore genus *Cicatricosisporites*. Bolkhovitina (1961) erected *Ruffordia aralica*

for dispersed spores which have widely spaced high muri but differ from spores of *R. goepperti* in overall smaller numbers of muri. Brenner (1963) placed all these spores in synonymy in *Cicatricosisporites aralica* comb. nov., but none of this procedure is admissible.

Genus PELLETIERIA Seward 1913

Remarks. The available material of the single macrofossil species *P. valdensis* is more extensive than that figured by Seward, but the necessary re-description cannot be included in this paper. We assume that Seward intended the specimen V2329 (pl. XII, fig. 12a) to be the holotype and herewith designate it as such in case there is any doubt. The specimen of plate XII, fig. 12b is on V2329 but has been partly destroyed in extracting spores, presumably by Seward; on the same rock specimen are the originals of Seward's text-fig. 4A and G but 4B-E have not been located. The specimen of text-fig. 4F (now damaged) is on slide V2329b; that of text-fig. 3B is on V2368, text-fig. 3A on V51843, and text-fig. 3C on V51840.

Pelletieria valdensis Seward 1913 (spores)

Plate 44, figs. 1-8; Plate 45, figs. 1-7

1913 Seward, p. 91, pl. 14 fig. 5, text-fig. 2B.

Holotype. Although Seward's wording (1913, p. 92, para. 2) may be taken to suggest that the specimen of his text-fig. 3B (V2368—Rufford Coll.) provided the spores, it seems certain from all other evidence that they came from V2329. We have found the original of Seward's photograph (1913, pl. 14, fig. 5) on slide V2329a and we re-figure it as the holotype (Pl. 44, fig. 4). It has not been possible to identify the obliquely viewed specimen of Seward's text-fig. 3B.

Locus typicus. V2329 and V2368 are both labelled Ecclesbourne, nr. Hastings; V2329 is a coarse grey siltstone, unbedded, with maximum grain size 150 μ . These specimens must again come from the lowest Ashdown sand or Fairlight clay *e*.

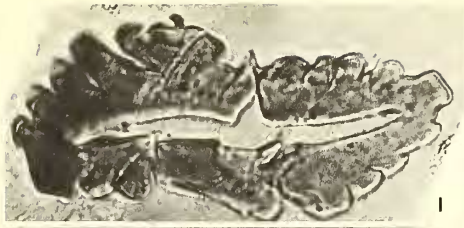
Material. Additional spores were taken from V2329 from an isolated spore mass very close to the original of plate XII, fig. 12b (Seward 1913).

EXPLANATION OF PLATE 44

Figs. 1-8. *Pelletieria valdensis* Seward; spores taken from specimen V2329 BMNH, $\times 1000$. 1-2, Sections parallel to polar axis, through laesura (2, near outer termination of laesura); prep. V2329j, OR 33.3 119.9 and 31.5 114. 3, Distal aspect, high focus; prep. V2329i, OR 37.8 117.6. 4, Holotype, proximal aspect; Seward's prep. V2329a, OR 28.7 118.9. 5-6, Equatorial aspects, prep. V2329f. 5, Showing profile of muri; OR 42.6 117.9. 6, Laesura open; OR 35.3 115.3. 7, Small specimen, equatorial aspect with optical section of proximal exine; prep. V2329a, OR 38.7 125.8. 8, Equatorial aspect; prep. V2329h, OR 35.7 117.8.

EXPLANATION OF PLATE 45

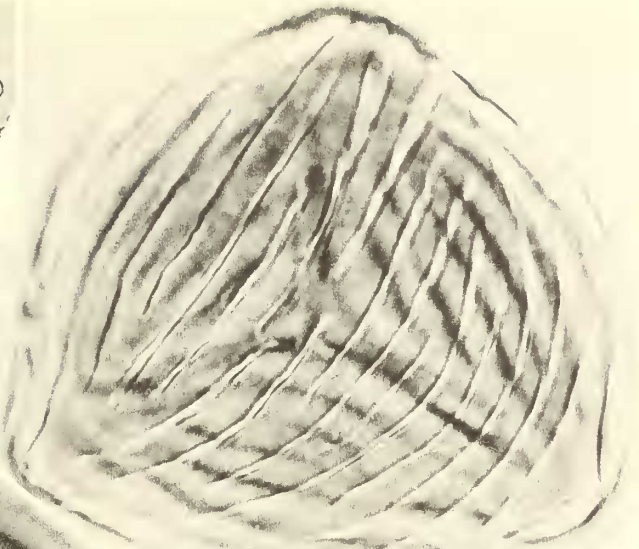
Figs. 1-7. *Pelletieria valdensis* Seward; spores taken from specimen V2329 BMNH, $\times 1000$. 1-2, Sections perpendicular to polar axis; prep. V2329j, OR 29.4 113.9 and OR 51.5 107.7. 1, Distal (slightly oblique). 2, Proximal face showing depression bordering laesurae. 3, Proximal aspect, high focus; prep. V2329g, OR 47.8 118.7. 4, Distal aspect; prep. V2329g, OR 40.7 121.7. 5-7, Sections parallel to polar axis; prep. V2329i, OR 50 111.8, OR 45 112.5, OR 42.3 112.3.



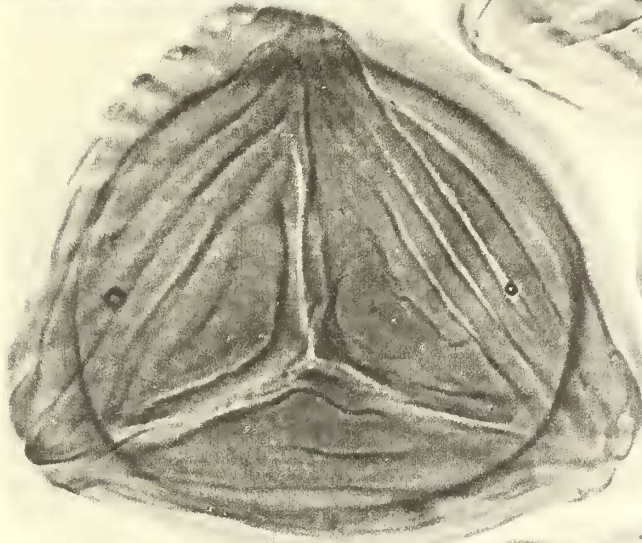
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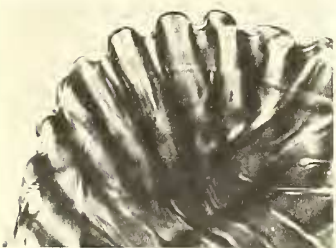
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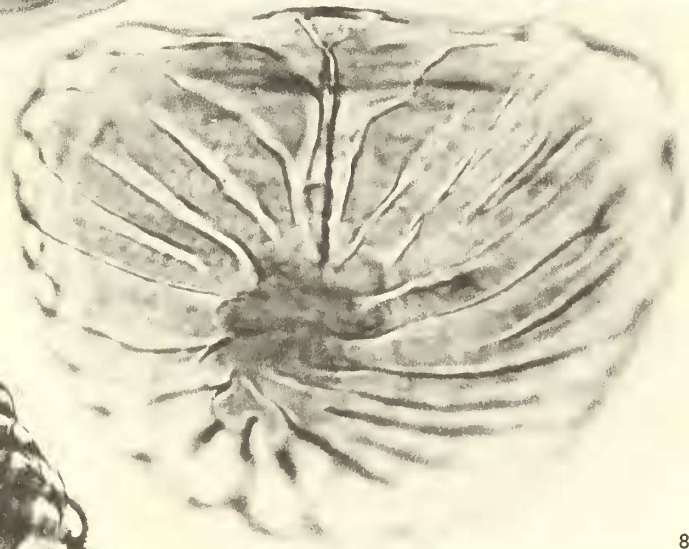
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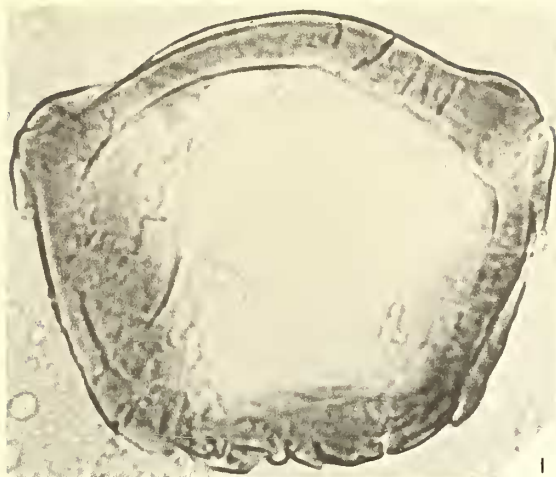
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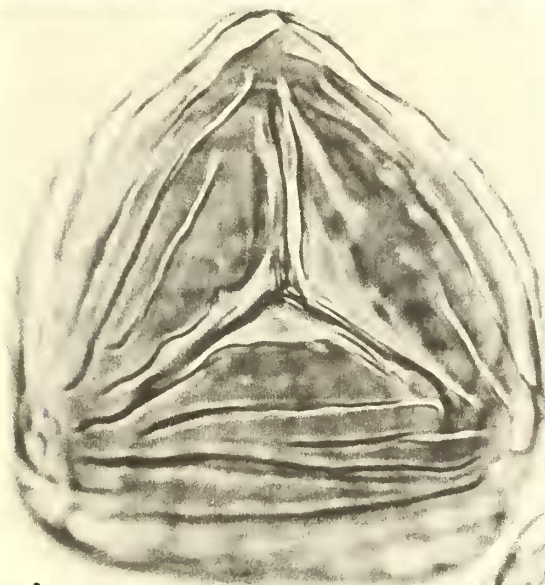
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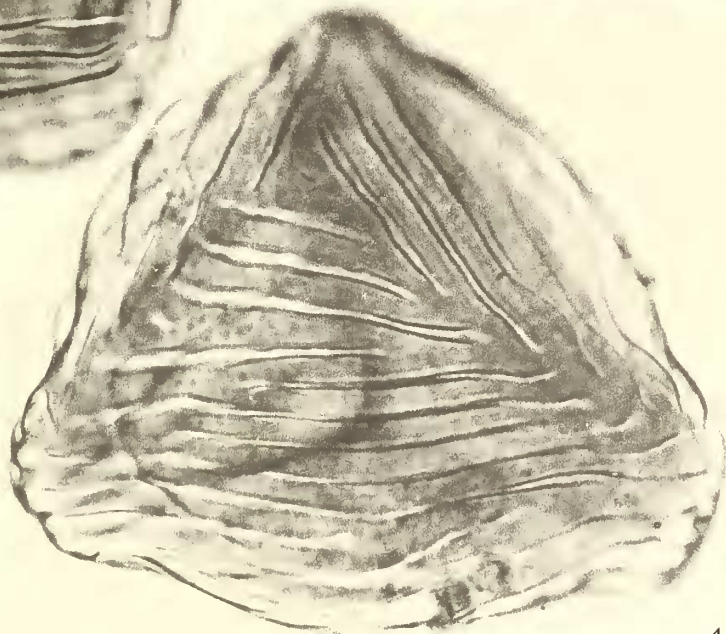
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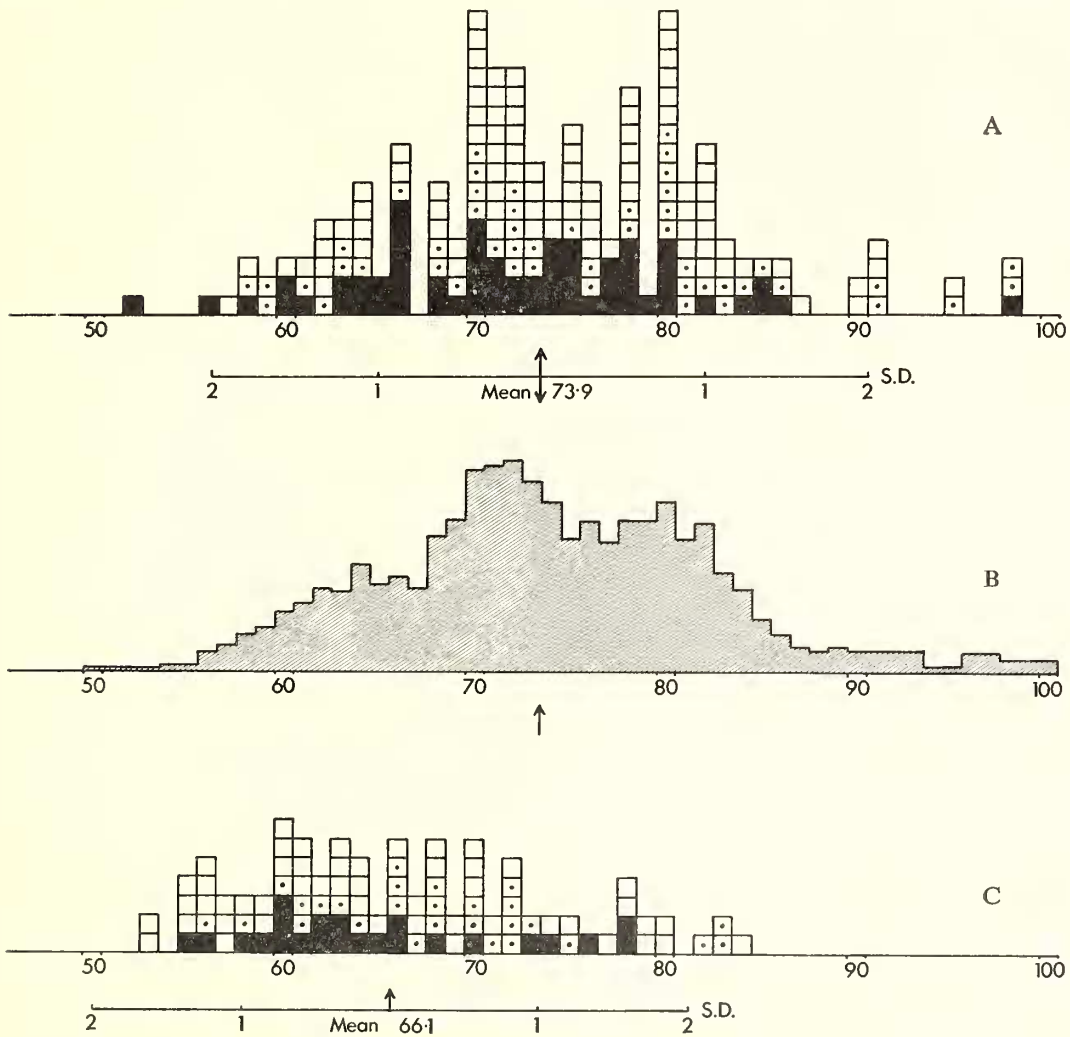


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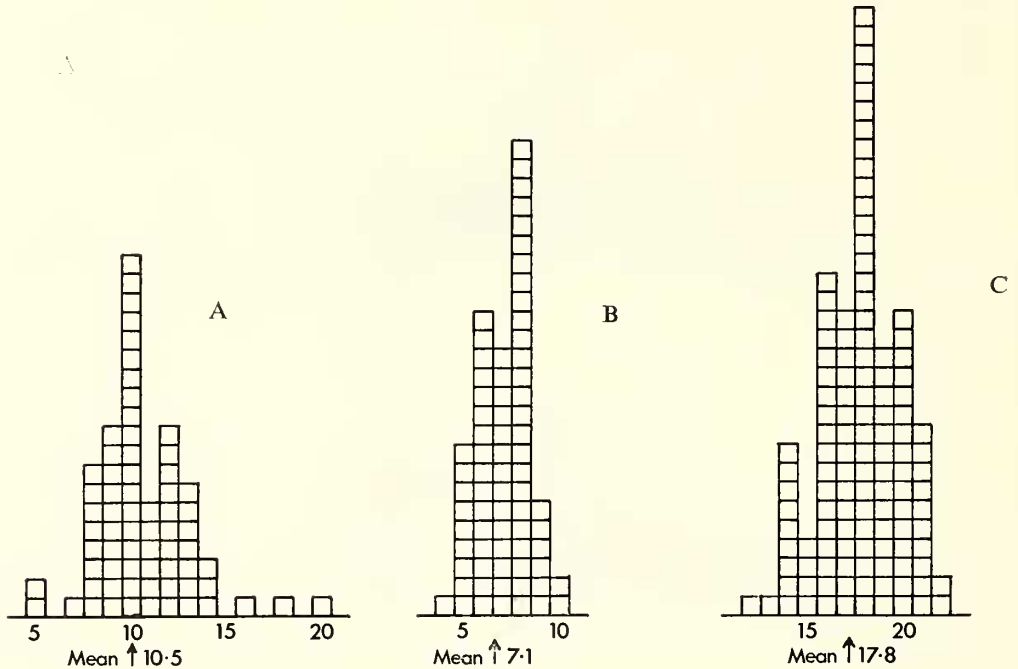
Emended diagnosis. Trilete spores with rounded triangular amb. Laesurae simple and with thin lips, of medium length flanked by variably deep and narrow areas of negative sculpture. Proximal and distal surfaces bear a regular canaliculate sculpture, best



TEXT-FIG. 3. Frequency distribution histograms of maximum diameters in microns, of spores of *Pelletieria valdensis*. A, New preparation (V2329f), 200 specimens; standard deviation 8.5μ , coefficient of variation 12 per cent. B, Five point moving average from the data of A. C, Seward's preparation (V2329a), 100 specimens; standard deviation 7.7μ , coefficient of variation 12 per cent.

described as of lumina 0.5 to 1.0μ wide and 4μ apart. The lumina, in three parallel inter-radial sets, do not coalesce but merely inter-finger in the radial regions, maintaining the latter as more rigid areas which affect the shape of the spore. Inter-radial exine thickness 6.5μ .

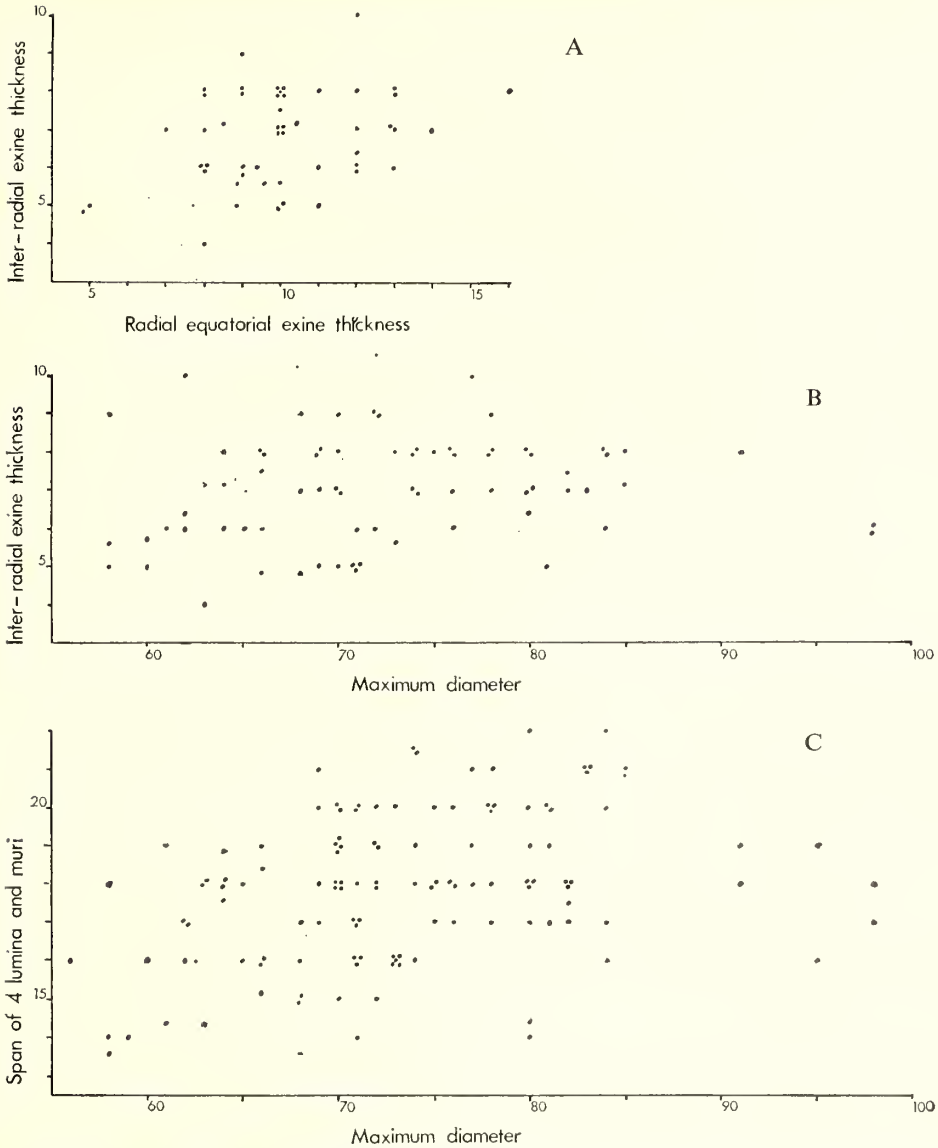
Dimensions. Diameter (200 specimens) 52–(74)–98 μ (new preparation V2329f); 80 per cent. of specimens have maximum diameter between 63 and 84 μ (text-fig. 3A). Specimens in polar aspect 25 per cent., equatorial aspect 30 per cent. Similar observations on 100 specimens from Seward's slide V2329a give diameter 53–(66)–84 μ (text-fig. 3C); 80 per cent. of values fall between 56 and 78 μ . Specimens in polar aspect 26 per cent., equatorial aspect 23 per cent. Values for Seward's specimens are again lower (see under *Ruffordia*).



TEXT-FIG. 4. Spores of *Pelletieria valdensis*; distribution histograms of measurements in microns with one square per specimen. Total numbers of specimens differ as not all characters are observable on every spore. A, Observed thickness of exine in radial equatorial region, 69 specimens. B, Inter-radial exine thickness, 73 specimens. C, Span covered by four lumina (and four muri), 123 specimens.

Description. The symmetry of the distal sculpture varies from the extreme seen in 24 per cent. of the specimens in which the triangle is centred on the distal pole (Pl. 45, fig. 4), through various intermediates to the sub-parallel lumina of Plate 44, fig. 3; it is doubtful whether this feature can have the taxonomic significance implied by Deak (1963). The span covered by four lumina (the same as the usual four muri) is recorded on text-fig. 4C, and plotted on text-fig. 5C. The resulting muri can be described as typically 3–(4)–5 μ wide, 3–4 μ high and flat-topped. The inter-radial exine thickness is recorded (text-fig. 4B) and plotted (text-fig. 5); such variability is of course much more easily observed in a thick exine such as in *Pelletieria*, than in one near the limit of optical resolution. The measured radial and inter-radial variable exine thickness depends on the degree to which the lumina are 'open' and this is affected by:

1. The directions of the lumina with respect to the amb (contrast Pl. 44, fig. 5, with a section, Pl. 45, fig. 7).

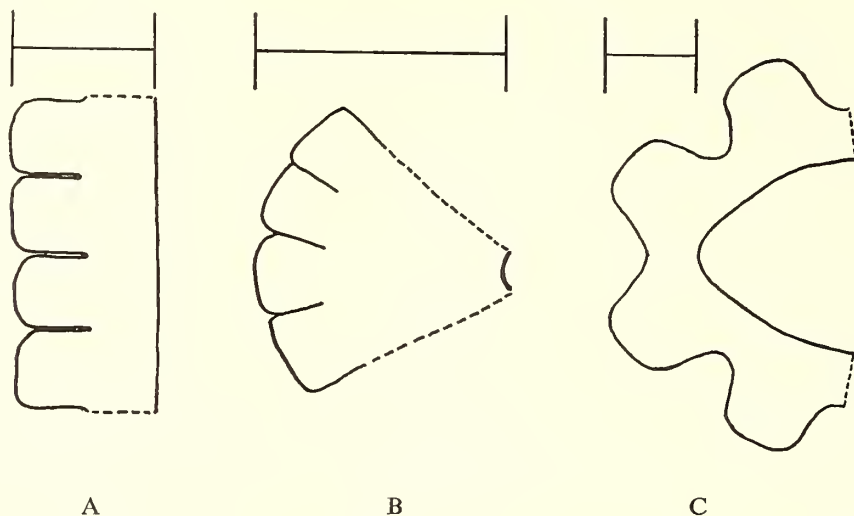


TEXT-FIG. 5A-C. *Pelletieria valdensis*; linear plots showing the possible relationships between some of the characters recorded in text-figs. 3 and 4, scales in microns.

2. The distance of the measurement from the radial areas where the lumina close; thus the diameter of the spore will affect this especially in small specimens.
3. The degree of inflation (in life?), and the compression of the specimen (in diagenesis).

On average (text-figs. 4, 5A) the radial thickness is fifty per cent. greater than the inter-radial. The opening of lumina up to an observed maximum of 90° is calculated to reduce

to two-thirds the depth of a lumen (text-fig. 6A, C), but this reduction will not explain the observed differences in exine measurements on many specimens. The simplest assumption is that the exine suffers some distortion but no change of volume when it is folded; the scale diagrams of text-fig. 6B-C show observed extremes of exine profile and measurements; compare with Plate 45, fig. 4. Text-fig. 6A compares with exine seen unfolded in Plate 45, fig. 7. By drawing on graph paper it was shown that all three



TEXT-FIG. 6. *Pelletieria valdensis*; diagrams of sections ($\times 2000$) of spore exine to explain variable exine thickness, bars show exine thickness as would be measured by optical section in polar view. A, Inter-radial exine, not folded; sections normal to direction of lumina. B-C, Exine folded at amb; plane of section containing polar axis. B, Radial. C, Inter-radial.

diagrams have the same cross-sectional area. Since this area is taken normal to the plane of folding (in text-fig. 6B, C), it will be proportional to the volume of a parallel element of exine. The observed differential exine thickness may be explained thus without postulating a taxonomically significant radial thickening. Since the orientation of the lumina affects the spatial properties of the spore, any asymmetry in the distal sculpture (76 per cent. of the specimens) often causes irregularity in the amb and in the exine measurements.

The tapering lips project above normal exine level near the proximal pole only; they are flanked by a variable negative area which closes or coalesces with a lumen when the lip membrane merges into the exine at the apparent limit of a laesura. We suggest that the negative sculpture, often deeper than a lumen, gives flexibility to an otherwise rigid proximal face. From Plate 45, figs. 2 and 5, and Plate 44, fig. 2, it can be seen that the laesurae extend lipless almost to the equator, well beyond what appears to be the limit in proximal surface view.

Comparison. Couper (1958) suggested that these spores were similar to his dispersed spore species *Cicatricosisporites dorogensis* but the size range and other features are

entirely different. A distinction is more necessary between this spore and *C. brevislaesuratus* Couper (type from Barremian/Aptian) which is even larger ($90\ \mu$) and is described as having an unsculptured contact face. Bolkhovitina (1961), perhaps on account of Couper's comparison, has inadvisedly (and wrongly) placed a number of unrelated dispersed spore species in this macrofossil genus.

The spores described from the Hastings Beds by Boodle (1895) were similar to those of *P. valdensis*; they occurred in a large spore mass but their provenance was not discovered.

Botanical Affinity. Neither the macrofossil remains nor the spores of *Pelletieria* are very close in detail to species of *Ceratopteris*, although the suggestion that the macrofossil may have been a water plant and not necessarily related to normal Schizaeaceae is worth exploring.

Genus SCHIZAEOPSIS Berry 1911b

Remarks. The genus is only valid from Berry's second paper (1911b), when he erected the necessary new species for the single specimen concerned (now USNM 3209).

Schizaeopsis americana Berry 1911 (spores)

Plate 46, figs. 1-8; Plate 47, figs. 1-10

1911a Berry, p. 193, pl. 12, figs. 2-6.

1911b Berry, p. 216, pl. 22, figs. 4-9.

Holotype. The original single photograph (Berry 1911b, pl. 22, fig. 4) is not recognizable; the drawings (pl. 22, figs. 5-9) are too generalized to be used further.

Locus typicus. Patuxent formation, Fredericksburg, Virginia, U.S.A.

Material. The rock specimen (USNM 3209) is a medium brown non-calcareous siltstone with plant fragments and the fairly large fertile frond described by Berry (1911b, pl. 22, figs. 1-3). A small part of the spore mass was taken from the tip of one of the central leaf lobes of the specimen; preparations USNM 3209 *g-j*.

Emended diagnosis. Spores almost spherical; amb convex rounded triangular. Laesurae trilete, short, simple, with raised thin ($0.5\ \mu$) lips. Whole surface covered by uniform narrow muri $1\frac{1}{2}\ \mu$ wide, $1\ \mu$ high, flat-topped; lumina $1\ \mu$ wide. The whole proximal face is covered by three inter-radial sets of muri; the equatorial region bears a single set of five or six circular muri parallel with the outer members of the proximal inter-radial sets. The distal surface is covered by a single set of parallel muri which converge abruptly opposite two radial areas and swing round parallel to the equatorial set in the third. Exine thickness $3-4\ \mu$ in distal and equatorial regions, thicker immediately round laesurae as a margo (*sensu* Harris 1955, p. 26).

Dimensions. Diameter (200 specimens) $44-(71)-87\ \mu$ (preparations USNM 3209 *g-j*); 80 per cent. of specimens have maximum diameter between $61\ \mu$ and $80\ \mu$. Specimens in polar aspect 16 per cent., equatorial 28 per cent. The records on text-fig. 7A, which are plotted on text-fig. 8A-C, show a numerically small but statistically significant group of small spores in this preparation. The group was distinguishable by eye, and proves to consist of small spores with thicker distal exines and narrower muri and lumina which had never opened at the laesurae (Pl. 46, figs. 5, 6).